

SHORT COMMUNICATION

Grasshopper egg mortality mediated by oviposition tactics and fire intensity

DAVID H. BRANSON¹ and LANCE T. VERMEIRE² ¹U.S. Department of Agriculture, Agricultural Research Service, Northern Plains Agricultural Research Laboratory, U.S.A. and ²U.S. Department of Agriculture, Agricultural Research Service, Livestock and Range Research Laboratory, U.S.A.

Abstract. 1. It is commonly assumed that arthropod species living or hibernating in the soil would not be affected by grassland fires, even though burning results in elevated surface and below-ground soil temperatures. The importance of elevated below-ground soil temperatures during fires on the survival of grasshopper eggs had not been examined.

2. The effects of simulated autumn grassland fires of varying intensities on below-ground egg mortality were examined with grasshopper species laying shallow egg pods (*Ageneotettix deorum*) and deeper egg pods (*Melanoplus sanguinipes*) to test the hypothesis that exposure to heat during fires was the mechanism responsible for population reductions in *A. deorum* following fire.

3. Species-specific oviposition characteristics mediated the effects of fire intensity on below-ground egg mortality. The results indicate that fires occurring in areas with at least 3100 kg ha⁻¹ standing crop biomass would be expected to significantly reduce populations of *A. deorum*, but not *M. sanguinipes*. No *A. deorum* eggs hatched in 12 of the 14 oviposition containers subjected to simulated fires approximating a standing crop biomass of 4500 kg ha⁻¹. This is the first study to link field observations of rangeland insect populations following fire to mechanisms related to below-ground egg mortality.

Key words. *Ageneotettix deorum*, burning, egg mortality, fire, grasshopper, *Melanoplus sanguinipes*, Orthoptera.

Introduction

Fire is both a naturally recurring event and common vegetation management tool in grasslands throughout the world and its ecological effects are numerous and complex (Wright & Bailey, 1982; Whelan, 1995; Pyne *et al.*, 1996). Fire can manipulate nutrient dynamics, soils, vegetation, and animals, with these effects being spatially and temporally variable within and among fires (DeBano *et al.*, 1998; Vermeire *et al.*, 2004b, 2005). Primary factors affecting community response are timing, frequency, and intensity of fire relative to the biology of organisms examined.

Burning has a range of negative and positive effects on grassland insects, with mechanisms operating over different

periods responsible for the outcomes (Warren *et al.*, 1987; Swengel, 2001; Panzer, 2002; Branson *et al.*, 2006). The timing and intensity of a fire can be particularly important relative to the developmental stage of an insect (Warren *et al.*, 1987). Fires can directly cause mortality or indirectly affect populations through post-fire modifications of food availability, habitat structure, microclimate, nutrient cycling, and primary production. However, most examinations of grassland insect responses to fire have failed to relate post-fire insect responses to either fire behaviour or other underlying mechanisms in an experimental fashion. As a result, past research has led to little predictive ability regarding the effects of burning on specific insect populations (Warren *et al.*, 1987; Whelan, 1995; Branson *et al.*, 2006). Limited research has been conducted with the explicit purpose of examining if grassland fires can be used to manipulate the population dynamics of abundant rangeland insects (Hunter, 1905; Haws & Coombs, 1982; Warren *et al.*, 1987; Watts *et al.*, 1989; Branson, 2005; Branson *et al.*, 2006).

Correspondence: David H. Branson, U.S. Department of Agriculture, Agricultural Research Service, Northern Plains Agricultural Research Laboratory, 1500 N. Central Avenue, Sidney, MT 59270, U.S.A. E-mail: dbranson@sidney.ars.usda.gov

It has been commonly assumed that arthropod species living or hibernating in the soil would not be affected by grassland fires (Anderson, 1973; Tschamtk & Greiler, 1995; Hoy, 1997), although quantitative data is largely lacking. While combustion is generally rapid in grassland fires, soil surface and shallow subsurface temperatures can reach levels considered lethal for most organisms (Wright & Bailey, 1982; Whelan, 1995). Heat transfer into the soil varies with soil texture, soil water content, fire intensity and duration of fire (Campbell *et al.*, 1995; DeBano, 1998). Prescribed fires in Oklahoma, U.S.A., which occurred when the grasshopper *Ageneotettix deorum* Scudder was in the egg stage, resulted in a two-thirds reduction of *A. deorum* (Vermeire *et al.*, 2004a). Vermeire *et al.* (2004a) hypothesised the reduction occurred from egg mortality resulting from elevated below-ground soil temperatures during the fire, as *A. deorum* egg pods are oviposited near the soil surface.

Grasshoppers are an important native component of North American grasslands and can be the most abundant and economically important insects in these systems (Hewitt & Onsager, 1983; Branson *et al.*, 2006). The effects of burning on grasshopper assemblages appear to differ between ecosystems and depend on the timing of the fire (Branson *et al.*, 2006), with both positive (Joern, 2004) and negative (Bock & Bock, 1991; Vermeire *et al.*, 2004a; Branson, 2005) effects on population densities. Changes in grasshopper populations following fire have been attributed to direct mortality (Bock & Bock, 1991; Vermeire *et al.*, 2004a) and indirect effects of fire-induced changes in host plant quality and plant community composition (Evans, 1984; Porter & Redak, 1996; Joern, 2004; Vermeire *et al.*, 2004a).

Although most species of prairie grasshoppers deposit eggs in the ground, oviposition depth varies from just below the soil surface to greater than 5 cm below the soil surface (Onsager & Mulkern, 1963; Pfadt, 2002). The number of eggs per pod and the orientation in which egg pods are oviposited also differs greatly between species (Onsager & Mulkern, 1963; Pfadt, 2002). As a result, temperatures in the vicinity of egg pods during a fire would be expected to differ based on oviposition characteristics. Additionally, the amount of combustible energy available (fuel load) controls surface temperatures and duration of heat during rangeland fire (Pyne *et al.*, 1996) and, thus, the amount of standing crop biomass is likely an important factor in determining if a fire causes egg mortality.

In the only direct examination of high temperature effects on egg mortality of North American grasshoppers, high rates of egg mortality occurred when egg pods of *Melanoplus sanguinipes* Fabricius were maintained in electric ovens at 50 °C for one hour or at 60 °C for 10 min (Parker, 1930). These laboratory results indicate that exposure to high temperatures for relatively short periods can kill grasshopper eggs. However, it is not known if grassland fires result in sufficient elevations of soil temperatures over long enough periods to cause mortality of grasshopper eggs oviposited below the soil surface, as hypothesised by Vermeire *et al.* (2004a).

In the work reported here, the effects of simulated autumn fire on below-ground egg mortality were examined using a grasshopper species which lays shallow egg pods (*A. deorum*) and a species laying deeper more vertically oriented egg pods

(*M. sanguinipes*). The importance of elevated soil temperature on the survival of grasshopper eggs had not been previously examined in the context of grassland fire. The experiment was designed to test the hypothesis that heat exposure during rangeland fire was the mechanism responsible for post-fire reductions in *A. deorum* populations (Vermeire *et al.*, 2004a; D. H. Branson & L. T. Vermeire, unpublished data) and whether oviposition behaviour mediated fire effects on egg mortality. By examining a range of fire intensities, predictions can be made regarding the fuel load associated with a given amount of egg mortality. No *A. deorum* eggs hatched in 12 of the 14 oviposition containers subjected to simulated fires that approximated a standing crop biomass of 4500 kg ha⁻¹, while *M. sanguinipes* hatching was not significantly affected. The results from this study indicate that fires occurring in areas with at least 3100 kg ha⁻¹ vegetative biomass would significantly reduce populations of *A. deorum*. This is the first study to link field observations of rangeland insect populations following fire to mechanisms related to below-ground egg mortality and has implications for the use of fire as a means of manipulating grasshopper population densities.

Materials and methods

Species descriptions

Ageneotettix deorum is widely distributed throughout much of the western two-thirds of North America and is often a dominant species in grasshopper outbreaks in mixed-grass prairie (Pfadt, 2002). *Ageneotettix deorum* is a small-bodied grasshopper that lays small egg pods of 3–5 eggs parallel to the soil surface, typically in the top 0.6 cm of soil (Shotwell, 1941; Onsager & Mulkern, 1963; Branson, 2006). *Melanoplus sanguinipes* is widely distributed throughout much of North America, often reaching high densities on rangeland and crops (Pfadt, 2002), and is frequently the most abundant rangeland grasshopper in western North Dakota and eastern Montana (Onsager, 2000; Quinn *et al.*, 2000). In contrast to *A. deorum*, *M. sanguinipes* oviposits egg pods vertically and seals them with a dried froth plug near the soil surface, with the midpoint of the egg pod approximately 2 cm deep (Onsager & Mulkern, 1963; Pfadt, 2002). Egg pods of *M. sanguinipes* can contain as many as 34 eggs (D. H. Branson, unpublished data), although egg pods containing far fewer eggs are laid under resource-limited conditions (Branson, 2003a, b). In the northern Great Plains, both *A. deorum* and *M. sanguinipes* lay egg pods during summer and fall which enter diapause and hatch the following year (Pfadt, 2002). Heat exposure to grassland fire would be expected to be greater for the shallow, horizontally oriented egg pods of *A. deorum* than the deeper, better soil-insulated egg pods of *M. sanguinipes*.

Experimental methods

Intact soil cores were collected 6–8 cm deep using a standard 10 cm golf cup hole cutter at a mixed-grass prairie location in western North Dakota, U.S.A., in early August 2004. Cores

were placed into 500 ml plastic cups of nearly equal dimensions to function as oviposition cups. Adult *A. deorum* and *M. sanguinipes* were caught nearby, separated by species, and placed in insect rearing cages containing oviposition cups. The cages were placed inside an insect rearing room at 30 °C with a 16 h/8 h light/dark cycle. Caged populations were maintained at a set ratio of four females per oviposition cup, with newly caught individuals added as necessary. Grasshoppers were fed romaine lettuce, greenhouse-grown wheat seedlings, and wheat bran *ad libitum*. As *A. deorum* is a granivorous species (Pfadt, 2002), it received proportionally more wheat seedlings and wheat bran. Oviposition cups remained in the rearing cages for approximately 2.5 weeks. For each species, the first set of 28 oviposition cups was removed on 24 August and replaced with a second set of 28 oviposition cups that was removed on 10 September. After removal, oviposition cups were watered until moisture penetrated to ~4 cm. Oviposition cups remained in the insect rearing room at 30 °C for an additional two weeks to allow eggs to reach their maximum pre-diapause developmental state and subsequently maintained at 21 °C. No moisture was applied in the two weeks prior to the simulated fire. To determine soil moisture content at the time of the simulated fire, eight oviposition cups were weighed, placed in a drying oven at 100 °C for 48 h, and reweighed. Soil moisture content averaged less than 4%.

Four treatments were chosen to represent a non-burned control and three time-temperature curves simulating fire across a range of common grassland fuel loads (1700, 3100, and 4500 kg ha⁻¹). Simulation methods were developed from trials varying the height of the heat source and duration of heat exposure to match peak temperatures and approximate time-temperature profiles observed by Wright *et al.* (1976) during actual rangeland fires. The heat source was a propane heater (Mr Heater® model MH12T, Cleveland, Ohio, U.S.A.) pointed downward over an epoxy resin lab bench. Soil cups without grasshopper eggs were used to develop temperature profiles and determine height of heat source and duration of heat exposure required for each treatment following the methods of Campbell *et al.* (1995). Excess plant debris on the soil surface was clipped and removed to prevent ignitions and reduce variation in heat treatments among cups. Holes, 4.7 mm in diameter, were drilled horizontally at 6.3 and 19.0 mm below the soil surface, representing the midpoint depth for egg pods of *A. deorum* and *M. sanguinipes* respectively. An additional hole was drilled upwards at an angle to the surface to allow measurement of sea surface temperature. Three type-K thermocouples insulated with ceramic fiber and Inconel braiding (Omega Engineering Inc., Stamford, Connecticut, U.S.A.) were placed in the holes and connected to a Campbell Scientific 21X micrologger with a SM4M storage module (Campbell Scientific Inc., Logan, Utah, U.S.A.) to record time-temperature profiles at each depth. The burner was positioned to be ~5 cm above the soil surface and intensity was controlled with time of exposure. Exposure time was determined by placing cups beneath the heater until the desired peak surface temperature was reached, then removing the cup. Times required to achieve peak temperatures and approximate time-temperature curves observed for fuel loads of 1700, 3100, and 4500 kg ha⁻¹ were 9, 23, and 46 s respectively. The prescribed durations of heat exposure were verified with three replications

of each treatment (Fig. 1). Because the highest body temperature survived by animals is 50 °C (Whelan, 1995), temperature measurement was stopped when the surface temperature decreased below that point. Degree-seconds using a base of 55 °C were calculated for each treatment and depth to quantify exposure to potentially lethal temperatures (Table 1).

Each of the eight treatment combinations of fire intensity (4) and grasshopper species (2) were replicated 14 times. Seven of the 14 replicates for each treatment were from oviposition cups removed from rearing cages in August and the remaining seven cups were those removed in September. Heat treatments were

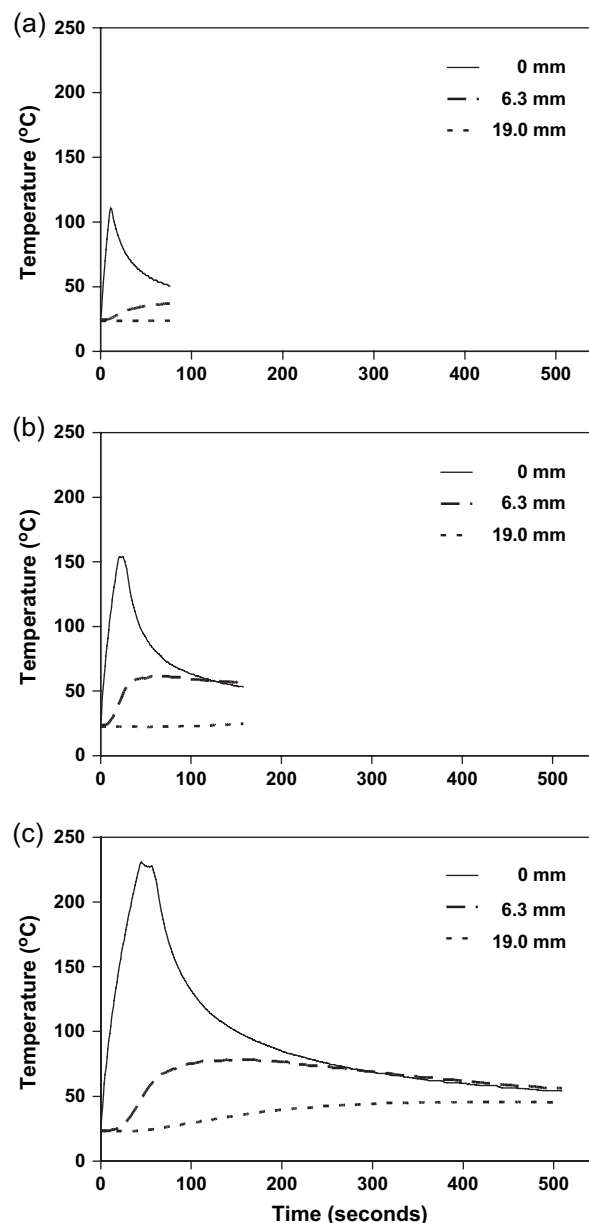


Fig. 1. Time-temperature profiles at three soil depths for heat treatments simulating fire with fuel loads of (a) 1700, (b) 3100, and (c) 4500 kg ha⁻¹ by applying heat for 9, 23, and 46 s respectively.

Table 1. Degree-seconds above the base temperature of 55 °C at 0-, 6.3-, and 19.0-mm soil depths for 9, 23, and 46 s of heat treatment approximating fuel loads of 1700, 3100, and 4500 kg ha⁻¹.

Soil depth (mm)	Degree-seconds > 55 °C		
	Heat treatment (s)		
	9	23	46
0	1110	4065	19 205
6.3	0	510	6067
19.0	0	0	0

applied to all oviposition cups within a two-hour period by individually placing the cups under the heater for the prescribed time.

One week after treatment, water was added to the oviposition cups until moisture penetrated ~4 cm. Soils in some oviposition cups of burned treatments were hydrophobic, which could have affected consistent water penetration. After one week, the cups were placed in a refrigerator at 8 °C for 3 months to break obligate diapause (Henry, 1985). The oviposition cups were placed in an insect rearing room at 30 °C with a 16 h/8 h light/dark cycle, and water was again added to the cups. Clear 950 ml plastic cages with a wire mesh top were placed on each oviposition cup and held in place with parafilm. Hatching grasshoppers were removed and counted daily, with species identification verified. Low pressure CO₂ gas was used to temporarily immobilise hatchlings and allow removal with a vacuum pump-powered aspirator. After no grasshoppers hatched for 10 days, egg pods were recovered from the oviposition cups. Egg pods were dissected under a dissecting microscope to determine the numbers of unhatched eggs and visibly charred eggs.

Statistics

The proportion of eggs that successfully hatched in each cup was used for the statistical analysis of treatment effects. A few oviposition cups of each species contained fully developed grasshoppers which did not successfully emerge from the soil and were counted as unhatched eggs in the analysis. As consistent oviposition could not be controlled in the rearing cages, an a priori decision was made to statistically analyze oviposition cups which contained four or more egg pods. Three oviposition cups were excluded from the statistical analysis in this manner. For each species, non-parametric Kruskal–Wallis analysis of variance was used to examine if burning significantly affected the proportion of eggs that hatched. If the Kruskal–Wallis analysis of variance was significant, additional pairwise comparisons planned before the experiment were used to relate grassland fuel loads with the proportion of eggs that hatched. Non-parametric Mann–Whitney tests were used to examine which fire intensity treatments led to a significant reduction in the proportion of eggs hatched, with *P*-values adjusted for multiple comparisons. Boxplots with median and quartile values were used to graphically represent the proportional egg hatch data. Statistical analyses were conducted using Systat 11 (Systat Software Inc. 2004) and SAS 9.1 (SAS Institute Inc. 2003).

Results and discussion

The proportion of *A. deorum* grasshopper eggs that hatched differed significantly between fire treatments (Kruskal–Wallis: $\chi^2_3 = 39.01$, $P < 0.001$). The proportion of eggs hatching was significantly lower in the medium and high intensity fire treatments, as compared to both the control and low intensity treatments (Fig. 2a). In addition, a lower proportion of eggs hatched in the high intensity fire treatment than in the medium intensity treatment (Fig. 2a). The mean proportion of eggs hatched was over 60% lower in the medium fire intensity treatment, which compares to a standing crop biomass of 3100 kg ha⁻¹, than in either the control or low intensity treatments. No eggs hatched in 12 of the 14 containers (Fig. 2a) in the high intensity fire treatment, indicating that fall fires in areas with at least 4500 kg ha⁻¹ standing crop biomass would be expected to largely eliminate *A. deorum* in the year following a fire.

The shallow depth and horizontal orientation of *A. deorum* egg pods resulted in high temperatures for egg pods in the medium and high intensity fire treatments (Fig. 1) where egg mortality was high. In the high intensity fire treatment, soil temperatures at the depth of *A. deorum* egg pods reached an average maximum of 78 °C, with a sustained temperature greater than 55 °C (Fig. 1; Table 1). On average, 35% of unhatched *A. deorum* eggs in the high intensity treatment were visibly charred, strong evidence that the application of simulated fire was the direct cause of egg mortality. Temperatures at egg pod depth in the medium fire intensity treatment reached an average maximum of 62 °C (Fig. 1). As *A. deorum* egg pods were often visible on the soil surface, eggs on the soil surface side of the horizontally oriented egg pods would be exposed to higher temperatures than measured at a depth of 6.3 mm. The proportion of eggs hatching relative to the control treatment was not significantly affected by the low fire intensity treatment, when soil temperatures 6.3 mm below the surface remained lower than 40 °C (Fig. 1).

The results appear to have direct relevance to naturally occurring late summer or fall fire events in grassland habitats where *A. deorum* is abundant. *Ageneotettix deorum* is most abundant in mixed-grass and bunchgrass prairie (Pfadt, 2002) where standing crop, including old dead material, ranges from 1250 to 5500 kg ha⁻¹ (Sims *et al.*, 1978). In the study by Vermeire *et al.* (2004a) where populations of *A. deorum* declined by approximately two-thirds following burning, herbaceous standing crop at the time of the prescribed fire ranged from 2800 to 3500 kg ha⁻¹. In this study, simulated fires with an intensity equivalent to an herbaceous standing crop of 3100 kg ha⁻¹ reduced the percentage of eggs hatching by 60%, similar to Vermeire *et al.* (2004a). In an eastern Montana mixed-grass prairie, late summer prescribed fire effects on *A. deorum* population densities varied with standing crop biomass (D. H. Branson & L. T. Vermeire, unpublished data). *Ageneotettix deorum* densities declined by ~80% following a prescribed fire occurring in a year when spring and early summer precipitation was near the long-term average. However, when standing crop biomass was low due to severe spring and early summer drought, late summer burning did not significantly affect *A. deorum* population densities.

Although grasshopper species exhibit strong preferences for open versus vegetated sites for oviposition (Stauffer & Whitman, 1997; Pfadt, 2002), Pfadt (2002) noted that *A. deorum* typically oviposits in areas with grass cover, while avoiding areas of bare ground. Such oviposition preferences would likely translate into egg mortality with lighter fuel loads than predicted. Fuel load is generally calculated at a scale much larger than the patch size

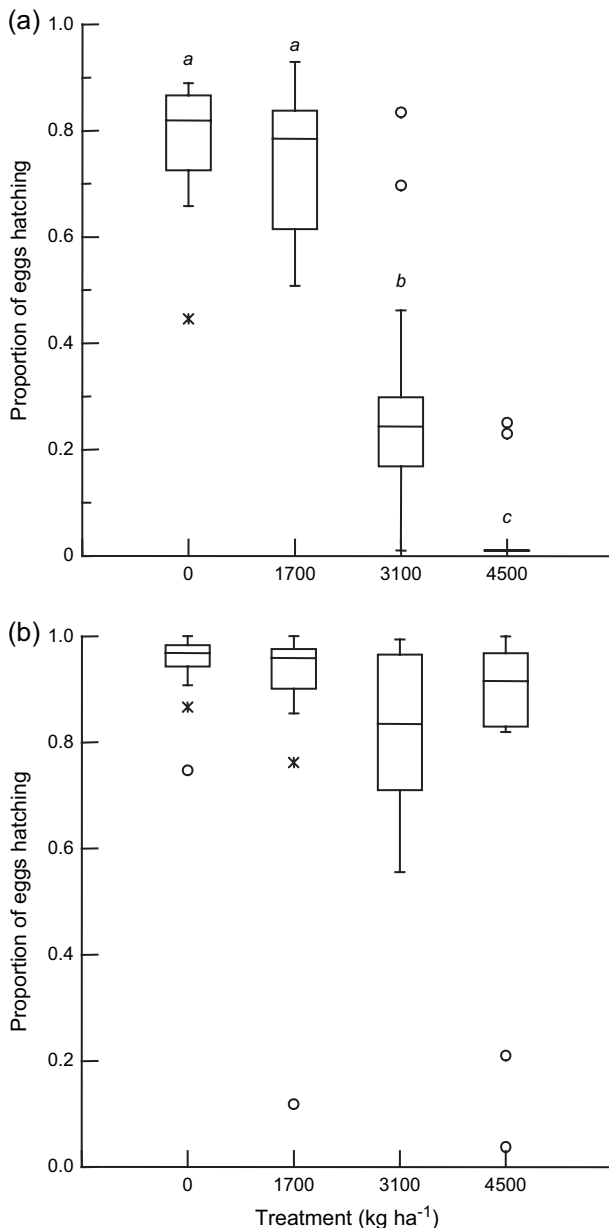


Fig. 2. Proportion of eggs which hatched for (a) *A. deorum* and (b) *M. sanguinipes* (median with 25% and 75% quartiles and upper and lower fences) in treatments simulating fire fuel loads of 0 (control), 1700 (9 s heat exposure), 3100 (23 s heat exposure), and 4500 kg ha⁻¹ (46 s heat exposure). Letters indicate values that differ significantly ($P < 0.05$) based on Mann-Whitney U tests. P -values were corrected for multiple comparisons using the Bonferroni correction.

for oviposition site selection. Therefore, fuel loads where *A. deorum* oviposits are likely to be greater than the average value across a plant community and a greater range of fuel loads could be predicted to reduce *A. deorum* populations. Likewise, species selecting for bare patches may experience lower fire intensity than may be expected based on average fuel loads.

Fire intensity did not significantly affect the proportion of *M. sanguinipes* eggs that hatched (Kruskal-Wallis: $\chi^2_3 = 5.51$, $P = 0.138$) (Fig. 2b), where the midpoint depth of egg pods is approximately 1.9 cm (Pfadt, 2002). Average temperatures at this depth increased above the ambient temperature only in the high intensity fire treatment (Fig. 1; Table 1). As a result, the deeper, vertically oriented egg pods of *M. sanguinipes* appear well protected from the effects of rangeland fires equivalent to a standing crop biomass of 4500 kg ha⁻¹. Although a few oviposition cups in burned treatments had a low percentage of eggs hatch (Fig. 2b), six oviposition cups in the high intensity fire treatment had greater than a 94% egg hatch. Only two of the 14 oviposition cups in the high intensity treatment had more than one visibly charred egg. Therefore, there are no indications that the high fire intensity treatment caused significant egg mortality in *M. sanguinipes*. As a result, natural fire events where standing crop biomass was 4500 kg ha⁻¹ or less would be not be predicted to cause significant direct mortality of eggs in *M. sanguinipes*.

The ability to predict insect responses to burning has been severely hampered by the failure of most studies to link observed responses to underlying fire behaviour mechanisms (Warren *et al.*, 1987; Branson *et al.*, 2006). This study is the first to link field observations of grasshopper population responses following fire with below-ground mechanisms of egg mortality responsible for the observations. Oviposition characteristics mediated the effects of fire intensity on below-ground egg survival. The relationship between heat treatments and *A. deorum* egg mortality predicts populations would be selectively reduced by fire intensities observed with 3100 kg ha⁻¹ or more fuel. The lower limit of increased *A. deorum* egg mortality was not identified, but should occur at fire intensities typical of fuel loads between 1700 and 3100 kg ha⁻¹.

Burning has been suggested as a means of manipulating insect population dynamics using naturally occurring ecological processes (Warren *et al.*, 1987; Branson *et al.*, 2006). It does not appear feasible to limit the population densities of grasshopper species that lay egg pods at depths similar to or greater than *M. sanguinipes* through fire-induced below-ground egg mortality when fuel loads are less than 4500 kg ha⁻¹. However, there are several common rangeland grasshopper species in western North America with midpoint egg pod depths of less than 1 cm (Pfadt, 2002). Such species may be susceptible to egg mortality resulting from elevated soil temperatures during burning, particularly if they preferentially oviposit near vegetative cover. A number of factors would impact the effectiveness of burning as a means of reducing population densities of *A. deorum* or other rangeland grasshoppers through below-ground egg mortality. Importantly, grassland fire intensity and behaviour are heterogeneous, even with abundant fuels (Pyne *et al.*, 1996). Most grasslands have a mix of bare ground and plant or litter cover which would result in spatial variability in surface and subsurface temperatures during grassland fires. As a result of this heterogeneity, it is unlikely

that grassland fires would create a local extinction of *A. deorum*. In addition to differences in fuel characteristics, fire intensity is responsive to wind, ambient temperature, relative humidity, and atmospheric stability, all of which may change during a fire. Transfer of heat into the soil is also affected by characteristics of the soil, including texture and water content (Campbell *et al.*, 1995; Whelan, 1995; DeBano *et al.*, 1998). Generally, heat is transported downward more rapidly for dry soils when surface heat exceeds 95 °C (Campbell *et al.*, 1995). Fires prescribed for vegetation management are typically applied under moist conditions to support plant growth, but may not be ideal for reducing population densities of a given grasshopper species through egg mortality. Dry periods, such as late summer and early autumn, may be more likely to result in high levels of below-ground egg mortality because of deeper heat penetration into the soil. About 75% of wildfires in the western U.S.A. historically occurred in July and August and continue to do so (Higgins, 1984; Westerling *et al.*, 2003). Although this experiment only examined fire-induced below-ground egg mortality, the direct effects of fire on above-ground stages can also strongly impact grasshopper population dynamics (Bock & Bock, 1991). An important consideration in terms of using fire as a management tool for grasshoppers or other insects is that vegetation responses to fire, either positive or negative, are likely to be of primary importance in determining management strategies.

The effects of fire-induced temperature increases on below-ground eggs have largely been ignored in previous research examining the effects of burning on grassland insects. In contrast to the common assumption that arthropod species living or hibernating in the soil at the time of a fire would not be affected by temporary increases in soil temperatures associated with grassland fires, the results of this study demonstrate that high rates of below-ground grasshopper egg mortality can result from grassland fires. Importantly, species-specific oviposition characteristics mediated the effects of fire intensity on below-ground egg mortality. The amount of standing biomass is predicted to be the determining factor in whether a given fire will lead to mortality of *A. deorum* eggs and potentially limit the population size of *A. deorum*, given that soil temperatures and the duration of heat during rangeland fire increase with the amount of standing biomass. This study demonstrates that fire can be used to selectively manipulate the population dynamics of an abundant grasshopper species and the ecological ramifications of fire on arthropod communities may extend well beyond the direct and indirect effects previously identified. Given the limited quantitative examinations of below-ground fire effects on egg mortality in insects, the results may have broader implications regarding the responses of insects to fire.

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